
ADAPTIVE RADIATION AND EVOLUTION OF BREEDING SYSTEMS IN *SCHIEDEA* (CARYOPHYLLACEAE), AN ENDEMIC HAWAIIAN GENUS¹

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ABSTRACT

A multi-disciplinary approach, including phylogenetic analysis, population biology, and quantitative genetics, has helped to elucidate the selective factors that have promoted speciation and shifts in breeding systems in *Schiedea* (Caryophyllaceae). *Schiedea* is the fifth largest lineage in the native Hawaiian flora and the most diverse lineage with respect to breeding systems. The genus is monophyletic and shares a common ancestor with a clade consisting of two arctic or boreal-north temperate species. Most inter-island colonizations were from older to younger islands, and most movement between islands led to sufficient isolation to result in formation of new species that are single-island endemics rather than species with multi-island distributions. Closely related species pairs occurring on older islands tend to differ in habitat and are isolated ecologically on the same island, while species pairs on younger islands tend to be in similar habitat on different islands. Speciation within this lineage has been associated with shifts in habitat, pollination system, and breeding system, including evolution of selfing (obligate autogamy, facultative autogamy), mixed mating systems, and dimorphism (gynodioecy, subdioecy, and dioecy). Dimorphic breeding systems appear to have been derived independently twice in *Schiedea*, and facultative autogamy and obligate autogamy have both evolved three times. The colonization of windy, dry habitats appears to occur before changes in sex allocation patterns, and the evolution of dimorphism in this lineage has been promoted by the combination of high inbreeding depression and high selfing rates. Many morphological traits associated with allocation to male and female function are highly heritable, and genetic correlations in general do not appear to constrain the evolution of dimorphism in *Schiedea*.

Key words: adaptive radiation, autogamy, breeding systems, Hawaii, inbreeding depression, resource allocation, *Schiedea*, selfing, sexual dimorphism.

Flowering plants reproduce with a remarkable diversity of breeding systems, even among closely related species, and the selective forces responsible for this diversity continue to be of great interest. Adaptive radiations in island systems have been particularly useful because the isolation of remote archipelagos has made it easier to identify selective factors and to discern evolutionary patterns (e.g., Wagner & Funk, 1995; Givnish & Sytsma, 1997; Grant, 1998). The Hawaiian Islands have been of particular interest in the study of plant mating systems because of the high incidence of dioecy in the flora. Worldwide, the average incidence of dioecy in angiosperm floras is about 4%–6% (Renner & Ricklefs, 1995), but the Hawaiian Islands have the

highest incidence of dioecy of any angiosperm flora studied (14.7%), followed closely by the New Zealand flora (12%–13%; Sakai et al., 1995a).

Phylogenetic studies have elucidated the relationships among taxa in some of the larger Hawaiian lineages (e.g., Baldwin et al., 1991; Baldwin, 2003; Givnish et al., 1995; Wagner & Funk, 1995; Weller et al., 1995; Sakai et al., 1997b; Kim et al., 1998; Ballard & Sytsma, 2000; Baldwin, 2003; Nepokroeff et al., 2003, 2005; Lindqvist et al., 2003; Carlquist et al., 2003; summary in Price & Wagner, 2004). Most Hawaiian groups lack a complete phylogeny, but because of the great isolation and small size of the native Hawaiian angiosperm flora (about 1020 species; Wagner et al., 2005a), it has been possible

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to identify plant lineages descended from a common colonist and examine evolutionary patterns in the Hawaiian Islands with respect to speciation (Price & Wagner, 2004), rarity and conservation status (Sakai et al., 2002), and breeding systems (Sakai et al., 1995a, b). The ability to identify lineages in the extant flora allows examination of traits correlated with breeding systems that are less confounded by phylogenetic relationships than analyses at the species or even the generic level (Sakai et al., 1995a; Steiner, 1988). Based on studies of these lineages, dioecious species in the Hawaiian Islands are descended from dimorphic colonists or from hermaphroditic colonists with in situ evolution of dioecy in the Hawaiian Islands. Ten percent of successful colonists had dimorphic breeding systems and gave rise to lineages with dimorphic species. These dimorphic lineages (with both dimorphic colonists and descendents) account for over half of the dimorphic species. Baker's law suggests that difficulties in obtaining mates will limit colonization by dioecious species more than hermaphroditic species, but the success of dimorphic colonists as well as biogeographic patterns within the Hawaiian Islands suggest that obtaining mates did not severely limit colonization by dimorphic species (Sakai et al., 1995a). The incidence of dimorphism is also high in the Hawaiian Islands because in at least 11 lineages dimorphism evolved from hermaphroditic colonists, accounting for about one third of the current dimorphic species. These lineages, with autochthonous evolution of dimorphism, tended to have higher diversification rates (more species per colonist) than either hermaphroditic lineages or dimorphic lineages (Sakai et al., 1995a). Analysis of lineages also indicates that breeding systems have evolved in the Hawaiian Islands not only in ways that promote outcrossing (e.g., dioecy), but also in ways that promote selfing (Weller et al., 1995; Price & Wagner, 2004; Weller et al., 2005).

While flora-level analyses of factors associated with breeding system evolution reveal general patterns, selective factors promoting speciation and the evolution of dimorphism may be most evident through studies of hermaphroditic lineages that evolved dimorphism after colonization of the Hawaiian Islands. We have focused on *Schiedea* Chamisso & Schlechtendal (Caryophyllaceae), a monophyletic lineage with a hermaphroditic ancestor in which 10 of the 34 species evolved dimorphism in the Hawaiian Islands. *Schiedea* is the fifth largest lineage in the native flora and the most diverse Hawaiian lineage with respect to breeding systems (Weller et al., 1995; Sakai et al., 1997b; Wagner et al., 2005b). We have used a multi-disciplinary approach, including phylo-

genetic analysis, population biology, and quantitative genetics, to understand both the genetic potential for the evolution of breeding systems in these species and the selective factors that have promoted speciation and shifts in these breeding systems.

SPECIATION AND PHYLOGENETIC ANALYSES OF *SCHIEDEA*

The genus *Schiedea*, with 34 species and 35 taxa, includes deciduous perennials in coastal habitats, sprawling subshrubs in mesic forests, woody shrubs in dry, mesic, and wet forest, rainforest vines, and small subalpine subshrubs. *Schiedea* exhibits the greatest diversity in breeding systems of any native Hawaiian angiosperm genus (Weller et al., 1990; Weller & Sakai, 1990; Weller et al., 1995; Sakai et al., 1997b; Wagner et al., 2005b), including hermaphroditic species that are obligately autogamous, facultatively autogamous, and partially selfing with mixed mating systems, as well as dimorphic species that are gynodioecious (females and hermaphrodites in populations), subdioecious (females, males, and a few hermaphrodites in populations), or dioecious (females and males in populations). In this section we review the changes in biogeography, habitats, and breeding systems that have occurred during diversification of the lineage. Shifts in breeding systems are associated with shifts in habitat and changes in pollination biology in *Schiedea*, and we have used phylogenetic analysis and the comparative method to help infer causal factors in the evolution of breeding systems (Weller & Sakai, 1999).

Earlier phylogenies of *Schiedea* based on morphological characters, chloroplast DNA, and ribosomal DNA restriction-site analysis (Wagner et al., 1995; Weller et al., 1995; Soltis et al., 1996; Sakai et al., 1997b) have been refined more recently using sequence analysis of ITS and ETS genes and a revised and expanded morphological data (Nepokroeff et al., 2005, unpublished). Only extant species were included in the study so that combined analyses could be conducted. Maximum parsimony analyses were performed using unweighted parsimony for the morphology and nuclear (ITS and ETS regions) data, both separately and combined. Maximum likelihood searches on the molecular data utilized an iterative approach to evaluate models and optimize model parameters for an initial set of trees resulting from parsimony analysis, and analyses were then performed under the fully defined model parameters (Nepokroeff et al., 2005). PAUP* v. 4.0b10 (Swofford, 2001) was used for maximum parsimony and maximum likelihood analyses. Bayesian analyses of morphological and molecular data were also conducted (Nepokroeff et al., 2005). The combined molecular and morpho-

logical data sets resulted in 222 characters informative in parsimony analysis. Using equal weighting of characters, 24 most parsimonious trees resulted, with a length of 613. The ITS and ETS sequences yielded a single likelihood tree, and a single Bayesian consensus tree was also produced. These trees were highly congruent in topology with each other and with the parsimony trees and are not shown here. Biogeography, habitat, and breeding system diversity were optimized using MacClade 4.0 (Maddison & Maddison, 2000) onto one of the 24 most parsimonious trees showing the fewest unresolved polytomies, although several weakly supported nodes indicate that conclusions about the number of evolutionary transitions are tentative.

Sequence analysis of ITS, ETS, *matK*, and *trnL-F* has provided a better understanding of the extant sister group to *Schiedea*. Based on these analyses, the extant sister group to *Schiedea* is strongly supported and consists of a lineage comprised of circumboreal-north temperate *Honckenya peploides* (L.) Ehrh. and *Wilhelmsia physodes* (Fischer ex Seringe) McNeill, a species with an Alaskan to northeastern Asian distribution (Nepokroeff et al., 2005). Analyses of the strict consensus tree of the 24 most parsimonious trees (Fig. 1) indicate that *Schiedea* is a strongly supported monophyletic lineage that arose from a single common ancestor of circumboreal or Alaskan origin. Although much of the phylogeny is only weakly supported, several areas with moderate to strong support are present, including a number of well-supported species pairs. In the strict consensus tree, with the exception of gynodioecious *Schiedea apokremnos* St. John, all other dimorphic species occur in a single moderately well-supported clade (sect. *Schiedea*) that also includes three hermaphroditic species. Within section *Schiedea*, there is moderate support for a terminal subclade of several dimorphic species (*S. salicaria* Hillebrand, *S. ligustrina* Chamisso & Schlechtendal, *S. adamantis* St. John, *S. kealiae* Caum & Hosaka, and *S. spergulina* A. Gray). Unfortunately, this section, which is of greatest interest in the evolution of dimorphism, is also one of the most poorly resolved parts of the tree, perhaps because it has evolved more recently than other clades.

BIOGEOGRAPHY AND PATTERNS OF SPECIATION

About 10% of angiosperm colonists in the Hawaiian flora have temperate affinities, including the ancestor of the lineage comprised of *Schiedea* (Fig. 2; Nepokroeff et al., 2005, unpublished). Although islands have been forming over the Hawaiian hot spot for the past 85 Ma (Clague, 1996), most colonization of the current high islands has occurred within the

past 5 Ma, because dispersal between islands was previously limited by an extended period when only small, low, widely spaced islands were formed (Price & Clague, 2002). The current islands with species of *Schiedea* range from the older islands of Nihoa and Kaua'i to the youngest island of Hawai'i (Fig. 3). In this analysis we consider Moloka'i, Lana'i, Maui, and Kaho'olawe as a single island (Maui Nui), because they were interconnected for more than 75% of their existence (Price & Elliott-Fisk, 2004). Species in the most basal clade of *Schiedea* (*S. membranacea* St. John and *S. helleri* Sherff) occur on the older island of Kaua'i, and the sister relationship of these two species is strongly supported. *Schiedea* appears to have colonized the older current major high islands, and the basal clades of *Schiedea* also exhibit the greatest morphological diversity (Wagner et al., 1995). The greater morphological diversity in these older clades may result from diversification into the greater range of environments that develop as islands age and from adaptation to more diverse modes of pollination. The higher probability of extinction of intermediate forms in the older clades may also emphasize differences among species.

Most inter-island colonizations appear to be from older to younger islands (Wagner et al., 1995), but a few back colonizations also may have occurred (e.g., from Kaua'i to Nihoa (*Schiedea verticillata* F. Brown in Christopherson & Caum), from Maui Nui to O'ahu (several dimorphic species), and from O'ahu to Kaua'i (*S. spergulina*)). In most cases, movement between islands led to sufficient isolation in space and time to result in formation of new species that were single-island endemics, rather than species with multi-island distributions. Only three species have multi-island distributions. *Schiedea globosa* H. Mann is a small subdioecious subshrub that grows only on coastal cliffs of O'ahu, Maui Nui, and Hawai'i and may disperse relatively easily between islands by rafting (Wagner et al., 1995); floating mats of *S. globosa* have been observed floating offshore of Moloka'i (Wagner et al., 2005b). Two other species (*S. hookeri* A. Gray and *S. nuttallii* Hooker) are both found on O'ahu and Maui Nui in diverse mesic forest.

Several Hawaiian lineages show inter-island colonization to younger islands followed by habitat diversification (Wagner & Funk, 1995). Species pairs that are well supported in phylogenetic analyses give some indication of the importance and differences in inter-island versus intra-island speciation in *Schiedea*. Most species pairs occurring on older islands are on the same island but differ in habitat, are isolated ecologically, and, in some cases, show pronounced morphological differentiation. Species pairs on younger islands tend to be in similar habitat on different

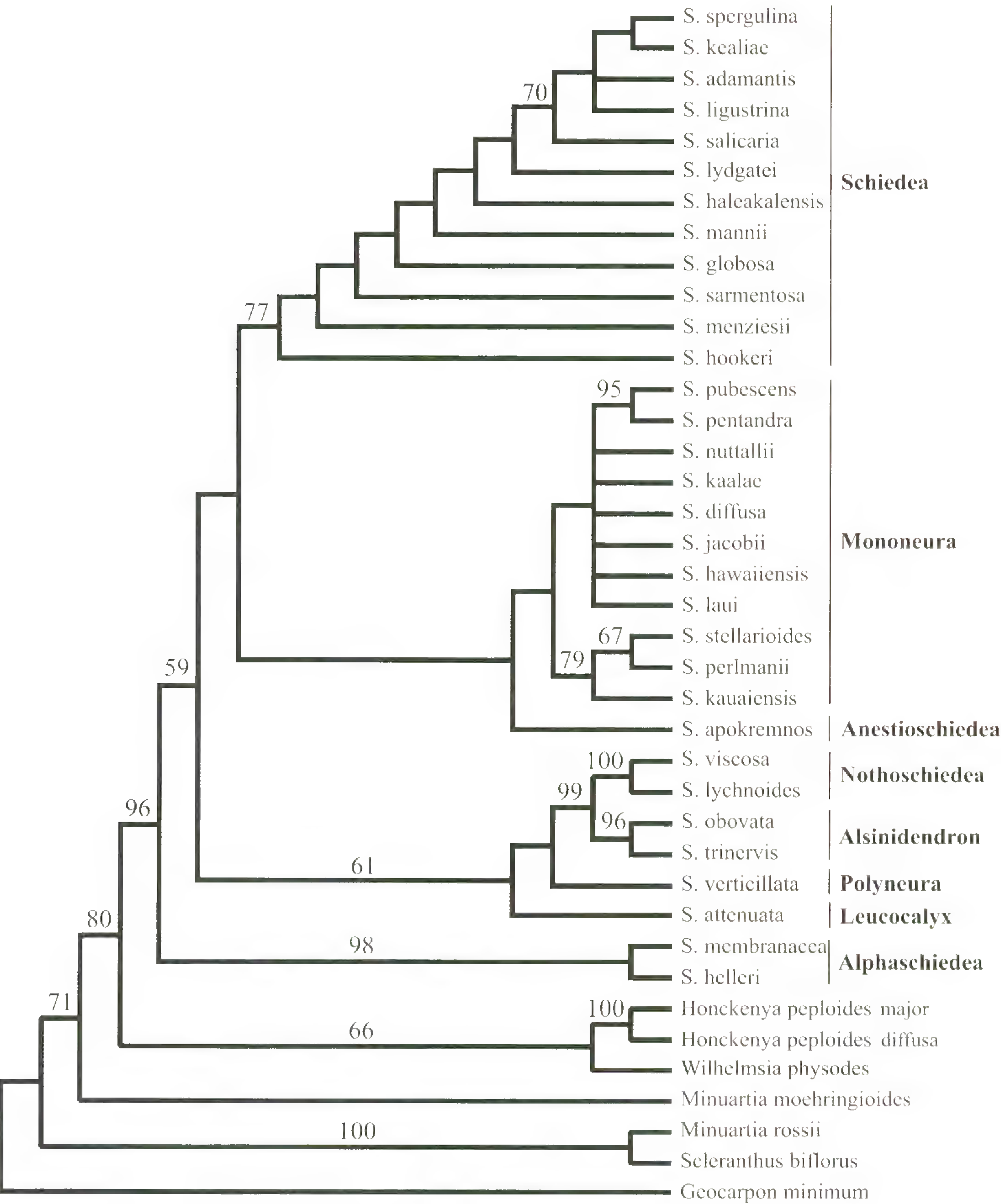


Figure 1. Strict consensus tree of 24 MP trees. Two major partitions of data were analyzed comprising sequence data from nrDNA ITS and ETS regions and morphology. Sixty-one morphological characters were scored, including 13 revised characters published in previous analyses (Weller et al., 1995; Wagner et al., 1995; characters listed in Wagner et al., 2005b). The sections of the genus are shown to the right of each clade. Bootstrap values greater than 50% are shown above the lines. Two extinct species, *Schiedea amplexicaulis* H. Mann and *S. implexa* (Hillebrand) Sherff, are omitted from the analyses (Wagner et al., 2005b). Species for which authorities are not given in the text include *S. haleakalensis* Mattf., *S. mannii* St. John, *S. sarmentosa* Degener & Sherff, *S. kaalae* Wawra, *S. stellarioides* H. Mann, *S. perlmanii* W. L. Wagner & Weller, *S. kauaiensis* St. John, *S. attenuata* W. L. Wagner, Weller & Sakai, *Honckenya peploides* subsp. *major* (Hooker) Hultén (Oregon), *Honckenya peploides* subsp. *diffusa* (Hornemann) Hultén ex V. V. Petrovsky (Baffin), *Minuartia rossii* (R. Brown ex Richardson) Graebner, *Minuartia moehringioides* (DC.) Mattf., *Scleranthus biflorus* Hook.f., *Geocarpon minimum* Mackenzie. Figure adapted from Wagner et al., 2005b.

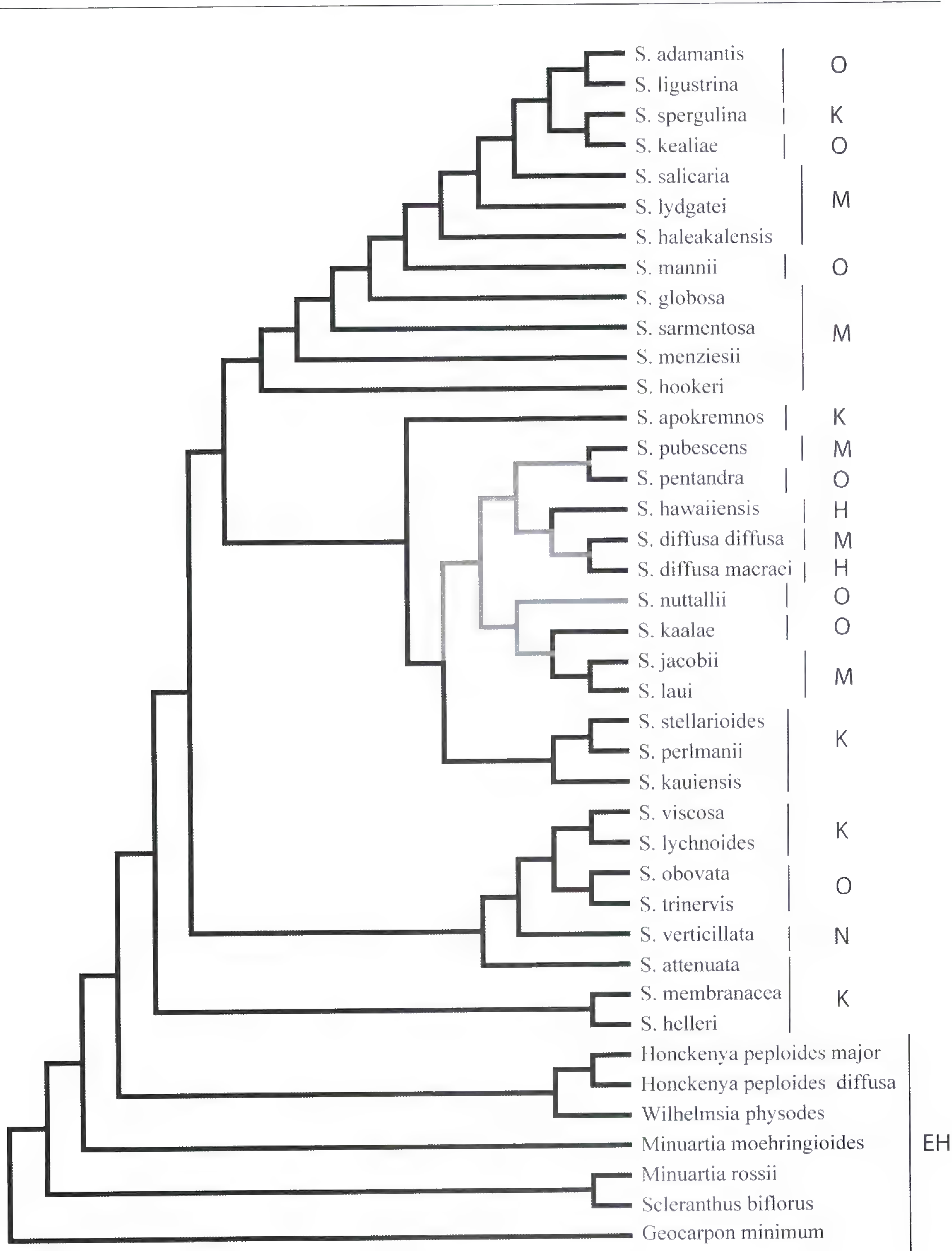


Figure 2. Biogeographic hypothesis for *Schiedea* using one of 24 most parsimonious trees reconstructed with MacClade 4.0 (Maddison & Maddison, 2000; figure adapted from Wagner et al., 2005b). Island abbreviations and ages: Nihoa (N, 7.3 Ma), Kauai (K, 4.7 Ma), Oahu (O, 3.0-2.6 Ma), Maui Nui (M, 2.0-1.2 Ma), Hawaii (H, 0.6-ongoing Ma), Extra-Hawaiian (EH). For species with multi-island distributions, coding indicates the island where it is most likely that the species evolved. Equivocal regions are indicated in gray.

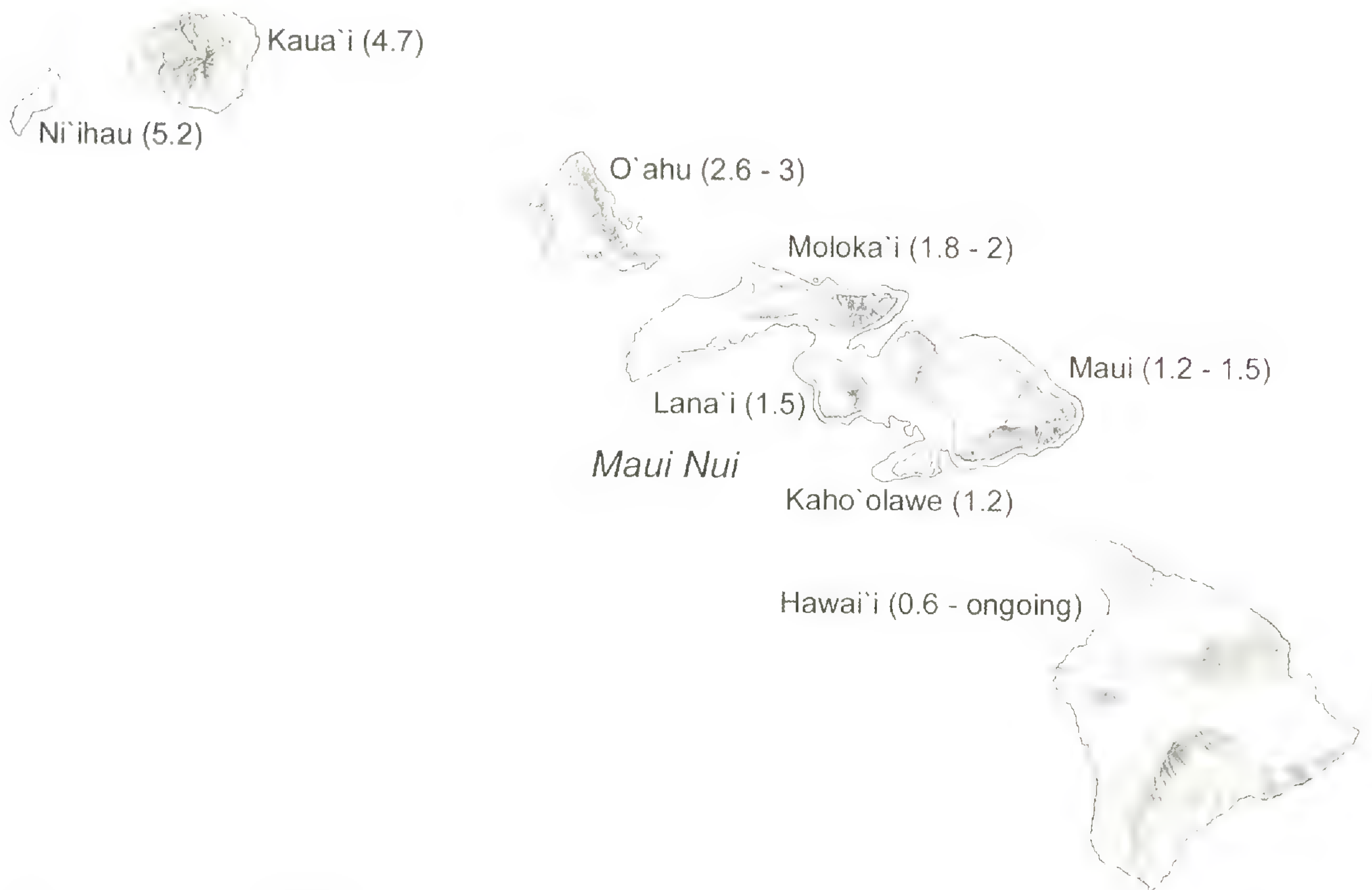


Figure 3. Map of the Hawaiian Islands, with island age in millions of years. Nihoa (7.3 Ma) occurs to the northwest of the islands shown.

islands and show less morphological differentiation. On the older island of Kauai, *S. membranacea*, a perennial herb, occurs in the mesic forest of several valleys, while closely related *S. helleri* is a vine found at higher elevations in wet montane forests. In the four species of the former genus *Alsinidendron* H. Mann, inter-island dispersal preceded differentiation in habitat. On Kauai, *S. viscosa* H. Mann and *S. lychnoides* Hillebrand are separated by elevation and habitat, although there is some geographic overlap. *Schiedea viscosa* occurs at slightly lower elevations in diverse mesic forest in limited areas, while *S. lychnoides* occurs throughout higher elevation wet forests on Kauai. On Oahu, *S. obovata* (Sherff) W. L. Wagner & Weller occurs in mesic forest at lower elevations throughout the Wai'anae Mountains, while *S. trinervis* (H. Mann) Pax & K. Hoffmann is found only in higher elevation wet forest in the northern Wai'anae Mountains. In the five species pairs on younger islands, both species occur in similar habitats, but geographical isolation has occurred through dispersal to different islands or mountain ranges on the same island (or former island in the case of Maui Nui). Two of these pairs occur in wet habitats (*S. jacobii* W. L. Wagner, Weller & Medeiros and *S. laui* W. L. Wagner & Weller on Maui Nui (Maui and Molokai, respectively); the two subspecies of *S. diffusa* A. Gray, *S. diffusa* subsp. *diffusa* and *S. diffusa* subsp. *macraei* (Sherff) W. L. Wagner &

Weller on Maui Nui and the island of Hawaii). One pair occurs in mesic habitat (*S. pentandra* W. L. Wagner & E. Harris and *S. pubescens* Hillebrand on Oahu and Maui Nui, respectively), and one pair occurs in dry habitats (*S. spergulina* and *S. kealiae* on Kauai and Oahu, respectively). Although both *S. ligustrina* and *S. adamantis* occur on Oahu in dry habitats, there is clear geographical separation by mountain ranges. *Schiedea ligustrina* occurs throughout the Wai'anae Mountains (formed 3.2–2.5 Ma) in western Oahu in dry forest to diverse mesic forest, often on cliffs. *Schiedea adamantis* occurs in a single population on steep dry slopes of open shrubland on Diamond Head crater in southeastern Oahu (formed about 0.5 Ma; Juvik & Juvik, 1998). More definitive biogeographical patterns of other *Schiedea* species await better resolution of their phylogenetic relationships.

Several species may be undergoing directional selection for greater fitness in dry environments colonized relatively recently. For example, *Schiedea hawaiiensis* Hillebrand may have only recently shifted from mesic to dry habitat. It occurs in dry, high light environments, but exhibits morphological traits (large leaves, open pendent inflorescences, vining habit) and physiological traits (maximum levels of photosynthesis, water use efficiency) more characteristic of mesic site species (Mishio et al., unpublished). On younger islands, ecological divergence of species may also be

limited by the later development of geological features creating drier habitats. Wet habitats are present on younger islands as soon as they become high enough to intercept moisture-laden tradewinds, but the drier leeward slopes and cliffs preferred by many *Schiedea* species develop only after erosion and/or subsidence as the islands age (Walker, 1990a, b).

HABITAT SHIFTS AND CHANGES IN BREEDING SYSTEM

The spectacular adaptive radiation in breeding systems in *Schiedea* apparently evolved within the past 5–7 million years. The association of changes in breeding system with habitat shifts has made it difficult to discern cause and effect, i.e., to determine if changes in habitat have driven shifts in breeding system, or whether shifts in breeding system have allowed movement into new habitats. Based on character optimization, the ancestor giving rise to *Schiedea* appears to have been hermaphroditic, and the ancestral habitat of *Schiedea* was most likely mesic forest. Although *Honckenya peploides* is dioecious, *Wilhelmsia* Rehb. and other close outgroups are hermaphroditic, and it appears that dioecy was derived independently in *Honckenya* Ehrh. and also within *Schiedea* (Fig. 1; Nepokroeff et al., 2005). Dimorphic breeding systems appear to have been derived independently twice in *Schiedea*—in *S. apokremnos* and once in section *Schiedea*. Within section *Schiedea*, it appears that *S. lydgatei* Hillebrand is hermaphroditic by reversal, possibly through loss of females during colonization of Molokai. Facultative autogamy has evolved three times—once in the former genus *Alsinidendron*, in the species pairs *S. jacobii*–*S. laui*, and in *S. hawaiiensis*–*S. diffusa*. Each of these groups with facultative autogamy has also evolved obligate autogamy (*S. diffusa* subsp. *macraei*, *S. laui*, and *S. trinervis*). Evolution of autogamous breeding systems is also linked to changes in habitat. Diversification into wet habitats has occurred independently five times, and in several of these cases, a shift to facultative or obligate autogamy has occurred. The repeated independent evolution of autogamy with wet habitats may result from historically small population sizes in these species, with selection for closed pendent flowers that are less likely to be adversely affected by extremely wet conditions (Weller et al., 1998; Wagner et al., 2005b). Some exceptions occur to these patterns; *S. helleri* occurs in wet montane forest, but shows no indication of autogamy, and *S. hawaiiensis* occurs in dry forest, but is autogamous rather than sexually dimorphic.

Evolution of dimorphic breeding systems is also linked to changes in habitat (Fig. 4). In both cases, the

independent evolution of dimorphism is associated with a shift to dry habitat. All ten dimorphic species occur in dry and windy habitat and most hermaphroditic species occur in mesic to wet habitat. Four hermaphroditic species also occur in dry habitats, although *Schiedea lydgatei* may be hermaphroditic by reversal. This pattern, where all dimorphic species as well as a few hermaphroditic species occur in dry habitats (e.g., *S. menziesii* Hooker, *S. hawaiiensis*, and *S. verticillata*), suggests that the shift to dry windy habitats precedes the shift in breeding system to dimorphism, but that the evolution of dimorphism is not inevitable after a shift to dry habitats. Once the shift in habitat has occurred, selection may simultaneously favor the evolution of dimorphism as a mechanism to promote outcrossing as long as pollen is not limiting for females (Weller et al., 1998). The evolution of adaptations promoting wind pollination becomes critical with the loss of biotic pollination limiting pollen dispersal in these habitats (Rankin et al., 2002). Alternatively, wind-facilitated selfing may evolve because of low pollen production, as in *S. hawaiiensis*, a hermaphroditic dry-site species derived from a lineage of mesic-wet forest species with low pollen production.

SELECTIVE FACTORS IN THE EVOLUTION OF DIMORPHISM AND SELFING

Inbreeding depression, selfing rates, and resource allocation are all factors that can lead to changes in breeding systems by favoring either selfing or, alternatively, the separation of the sexes and the evolution of dimorphism in these species (reviewed in Sakai & Westneat, 2001). In cases with nuclear inheritance of male sterility, as in *Schiedea* (Weller & Sakai, 1991), theoretical models suggest that strong selection for dioecy may occur as a mechanism to promote outcrossing (Lloyd, 1975; Charlesworth & Charlesworth, 1978; reviewed in Geber et al., 1999; Weller & Sakai, 2005). If inbreeding depression (δ) is high, selfed progeny of hermaphrodites will have lower fitness than progeny derived from outcrossing. Unisexual individuals, usually females, will be favored because they produce outcrossed progeny with relatively higher fitness than the selfed progeny of hermaphrodites. Under the simplest conditions, females will be favored if $k + s\delta > 0.5$, where k is the seed production of females relative to hermaphrodites ($k = 0$ if females and hermaphrodites produce equal numbers of seeds) and s is the selfing rate. Because dioecious species produce only unisexual individuals, inbreeding (with selfing as the most extreme form of inbreeding) is much less likely in dioecious species than in hermaphroditic species. Separate sexes may

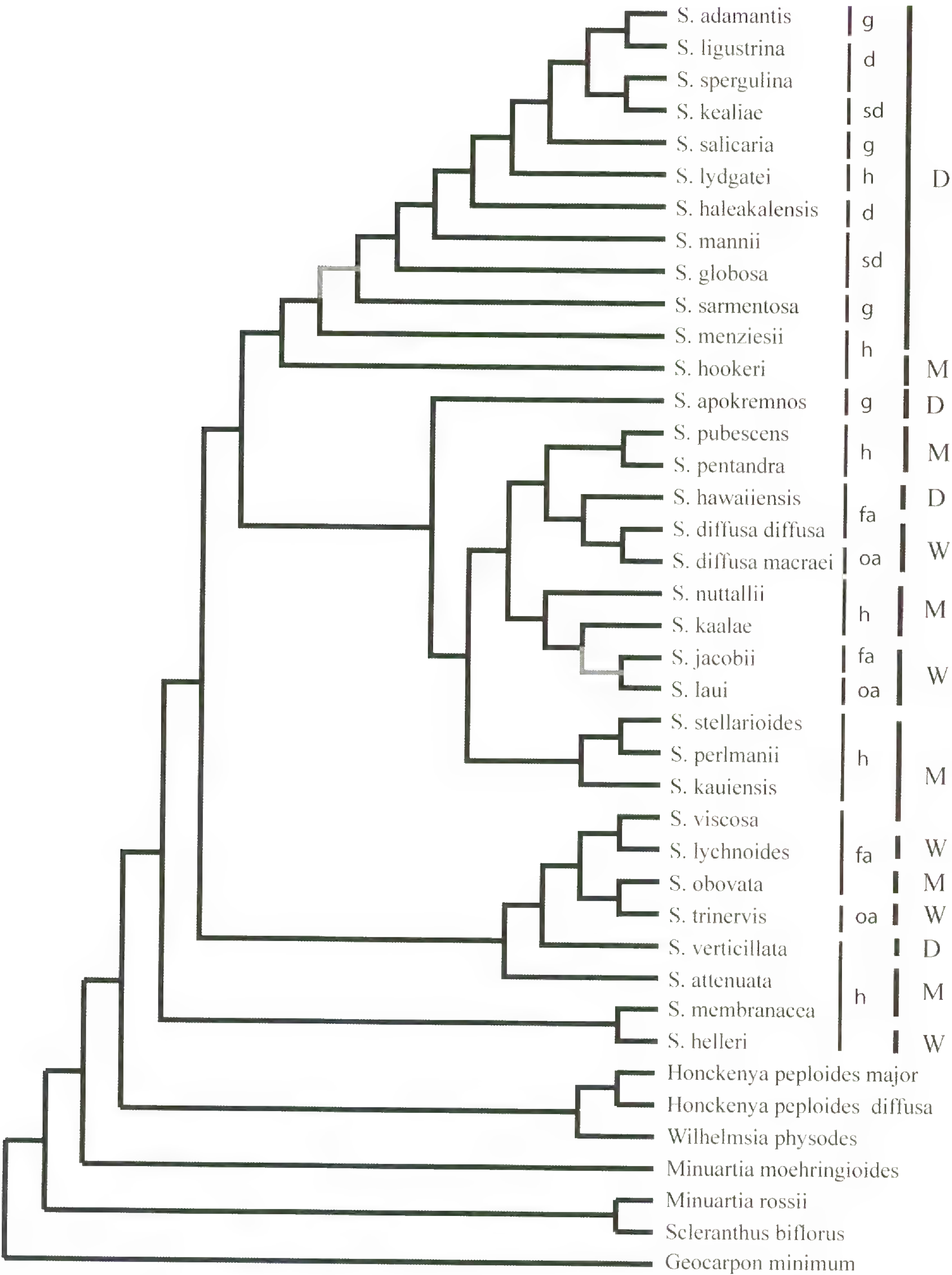


Figure 1. Breeding system evolution hypothesis for *Schiedea* using one of 24 most parsimonious trees reconstructed with MacClade 4.0 (Maddison & Maddison, 2000; modified from Wagner et al., 2005b). Habitats of species are shown in the bar to the right. Equivocal regions for breeding systems are indicated in gray. Habitats: D = dry slopes and cliffs; M = Mesic forest and shrubland; W = Wet forest. Breeding systems: g = gynodioecious; d = dioecious; sd = subdioecious; h = hermaphroditic; fa = facultatively autogamous; oa = obligately autogamous.

also be favored in the absence of high inbreeding depression and high selfing rates if females compensate for the lack of male function (pollen production) by producing more than twice as many seeds as hermaphrodites ($k = 1$; Charlesworth & Charlesworth, 1978; Lloyd, 1975). A combination of somewhat greater seed production by females and higher levels of selfing and inbreeding depression may also promote separate sexes.

Resource allocation to primary sex traits such as biomass of pollen and seeds will obviously change with the introduction of unisexual individuals in a population of hermaphrodites (i.e., the evolution of gynodioecy and dioecy from hermaphroditism). The more challenging problem has been to discover if these changes in resource allocation patterns are the driving force in the evolution of separate sexes, with subsequent changes in inbreeding depression and selfing rates, or alternatively, if changes in selfing rates and inbreeding depression occur first. The order of these changes is difficult to deduce in dioecious species, where changes both in resource allocation and in levels of inbreeding and inbreeding depression already have occurred. Gynodioecious species that are under continuing selection for changes in the frequency of females may offer more insights than dioecious species into the factors important in the evolution of both gynodioecy and dioecy.

Comparisons of six species of *Schiedea* species give some clues about the relative order and importance of changes in inbreeding depression, selfing rates, and seed production with the evolution of breeding systems in this lineage (Table 1; Norman et al., 1995, 1997; Sakai et al., 1997a; Culley et al., 1999; Rankin et al., 2002; Weller & Sakai, 2005; Weller et al., 2005). Measurements of seed production were taken from field-collected inflorescences. Selfing rates were measured using starch gel electrophoresis on progeny grown in the greenhouse from field-collected seeds. Because most field sites occur on remote steep cliffs, levels of inbreeding depression were measured in the greenhouse on progeny resulting from controlled crosses involving self and outcross pollinations. Traits used to calculate inbreeding depression included the number of seeds per capsule following the controlled pollinations, percent germination, percent survival until flowering, and either the number of flowers per inflorescence or inflorescence biomass. The relative fitness of selfed progeny as a proportion of values for outcrossed progeny was calculated for each trait for each family and used in a multiplicative fitness function. Inbreeding depression was calculated as 1-relative fitness. Our inbreeding depression studies of these perennial plants in the greenhouse probably underestimate the levels

of inbreeding depression expressed in the field over more than one flowering season in presumably harsher field conditions.

Schiedea membranacea is a member of the basal clade of the lineage and has a hermaphroditic breeding system. It is a perennial herb endemic to Kaua'i that grows in mesic environments typical of hermaphroditic species. *Schiedea membranacea* has a high level of outcrossing (low selfing rate) that prevents expression of the high inbreeding depression detected following controlled crosses in the greenhouse (Culley et al., 1999). Measures of genetic diversity (number of alleles per locus, percent of loci polymorphic, and percent heterozygosity) also are consistent with other outcrossing species (Weller et al., 1996). *Schiedea membranacea* is apparently biotically pollinated, with a relatively low pollen : ovule ratio and an open inflorescence (Table 1). Because of the low selfing rate, expression of inbreeding depression is low, and the hermaphroditic breeding system in this species is apparently stable.

In contrast to *Schiedea membranacea*, *S. viscosa* has a stable hermaphroditic breeding system because it has a high selfing rate, but much of the inbreeding depression characteristic of outcrossing species has been eliminated from these populations (Weller et al., 2005). Typical of populations that are historically selfing, the pollen : ovule ratio is extremely low, and *S. viscosa* also has very low measures of genetic diversity (Table 1). *Schiedea viscosa* (formerly in the genus *Alsinidendron*) is a rare hermaphroditic vine that occurs in mesic habitats of Kaua'i. The flowers of *S. viscosa* are pendent and remain relatively closed, traits that may be adaptive in rainy conditions and that may have promoted the evolution of selfing. *Schiedea viscosa* also produces nectar (0.64 μ l/flower/24 h in the greenhouse), suggesting an earlier history of biotic pollination (Weller et al., 1998).

Two gynodioecious species illustrate the changes that may occur with an increase in the frequency of females in populations. *Schiedea salicaria*, a gynodioecious species with a low frequency of females (13%), is found in dry windy habitats of the West Maui Mountains. *Schiedea adamantis* is also gynodioecious with a higher frequency of females (39%), and is found on the more recent dry slopes of Diamond Head Crater on O'ahu. In these two species, greater differentiation between females and hermaphrodites in primary and secondary sex traits occurs in *S. adamantis* (Golonka et al., 2005). In *S. salicaria*, females and hermaphrodites show only slight differentiation in floral and inflorescence traits and nearly identical seed production (Weller & Sakai, 2005). In *S. adamantis*, females produce 2.3 times more seeds than hermaphrodites in the field. This occurs because

Table 1. Habitat, breeding system, selfing rate, inbreeding depression, and differences in resource allocation for six species of *Schiedea*. For methods see Norman et al., 1997; Weller et al., 1998; Culley et al., 1999; Rankin et al., 2002; Weller et al., 2005. Resource allocation differences between females and hermaphrodites cannot be calculated in hermaphroditic species. Number of flowers per inflorescence and inflorescence condensation were not measured in *S. viscosa*. Inflorescence condensation is the number of flowers/inflorescence/inflorescence length in cm. Small populations are < 30 individuals; large populations are > 100 individuals. Estimates of genetic diversity (mean number of alleles per locus, percentage of loci polymorphic, and mean heterozygosity) were based on 24 to 39 plants per population (Weller et al., 1996).

Habitat	<i>S. membranacea</i> mesic forest herb	<i>S. viscosa</i> mesic forest vine	<i>S. salicaria</i> dry shrubland shrub	<i>S. adamantis</i> dry shrubland shrub	<i>S. menziesii</i> dry shrubland shrub	<i>S. lydgatei</i> dry shrubland shrub
Breeding system	hermaphroditic	hermaphroditic	gynodioecious (13% F)	gynodioecious (39% F)	hermaphroditic	hermaphroditic (reversal)
Pollinator	biotic	biotic	wind	wind	not adapted to wind	biotic (moth)
Ovule (N)	29	122	35	17	46	32
Pollen (N)	8,037	3,122	14,756	22,177	13,935	11,211
P:O ratio	282	25	419	1308	304	351
Pollen size (μ)	32.5	38.0	33.5	28.7	34.8	32.5
N fl/inflo	94.3	—	30.1	54.5	26.6	24.5
Inflorescence length (cm)	42.3	—	6.9	5.2	4.4	10.6
Inflorescence condensation	2.2	—	4.5	10.5	6.0	2.3
Nectar (μl/24 h)	0.030	0.643	0.236	0.155	0.385	0.325
Selfing rate	low (0.3)	high (presumed 1.0)	high (0.7)	high (0.7)	high (0.8)	low (0.2)
Inbreeding depression	high (0.7)	low (0.0)	high (0.8)	high (0.6)	high (0.8)	high (0.6)
Allocation	—	—	no difference between F and H	F produce 2.3× more seeds than H	—	—
Population size	large	small	large	large	large	large
Mean N alleles/locus	3.0	1.0	2.2	1.6	2.7	2.7
% of loci polymorphic	66.7	0	77.8	22.2	77.8	88.9
Mean heterozygosity	0.366	0	0.305	0.077	0.340	0.322
Assessment	stable; outcrossing hermaphrodites	stable; facultative selfing	unstable; selection for females	unstable; selection for females	unstable; selection for females	stable; outcrossing hermaphrodites

females and hermaphrodites produce similar numbers of inflorescences and flowers per inflorescence in the field, but females produce far more capsules per inflorescence than hermaphrodites (Sakai et al., 1997a). *Schiedea adamantis* also shows much greater adaptation toward wind pollination, with a higher pollen : ovule ratio, smaller pollen grains, and more condensed inflorescence than *S. salicaria*. *Schiedea salicaria*, although wind pollinated, has pollen : ovule ratios, pollen grain size, and inflorescence architecture more similar to biotically pollinated species (Weller et al., 1998; Golonka et al., 2005).

Schiedea salicaria and *S. adamantis* also differ in levels of selfing and inbreeding depression. *Schiedea salicaria* has a mixed mating system, with a high selfing rate (0.7; Weller & Sakai, 2005), but with extremely high inbreeding depression (0.8; Sakai et al., 1989). The low frequency of females in *S. salicaria* is consistent with these estimates, although if selfing and inbreeding depression have been underestimated in these greenhouse studies, selection for increased representation of females may be strong. In contrast, *S. adamantis* has both high selfing rates and high inbreeding depression (Sakai et al., 1997a). In combination with the greater seed production of females, these rates of selfing and inbreeding depression suggest strong selection for females in *S. adamantis*. The predicted frequency of females (based on Lloyd, 1975) is 42%, remarkably close to the observed frequency of 39% (Sakai et al., 1997a). The low estimates of genetic diversity in *S. adamantis* suggest a severe population bottleneck in the past (Weller et al., 1996). More recently, the size of this population has fluctuated widely over the past 20 years, from a high of about 400 flowering plants to a current low of 2 plants because of extended drought and competition from alien species.

Schiedea menziesii, one of the few hermaphroditic *Schiedea* species growing in dry habitats, may be under selection for evolution of sexual dimorphism. Unlike other dry site species, *S. menziesii* does not appear to be well adapted for wind pollination (e.g., low pollen : ovule ratio) and shows no evidence of wind pollination in a wind tunnel (Weller et al., 1998). This species has both high inbreeding depression and high selfing rates, conditions that favor females in populations (Table 1; Rankin et al., 2002). Females occasionally occur in field-collected seeds grown in the greenhouse, but have not been detected in the field. Greenhouse crosses suggest that these females are a result of a mutation for male-sterility (Weller & Sakai, unpublished). Without biotic pollinators, females may not be able to establish and increase in the population without adaptations to wind pollination. The lack of adaptations for intrafloral selfing

suggests that the evolution of autogamy is unlikely, even with high selfing rates.

Schiedea lydgatei is another hermaphroditic species found in dry habitats on Moloka'i, and based on phylogenetic evidence, appears to be hermaphroditic by reversal from a sexually dimorphic breeding system. Unlike *S. menziesii*, *S. lydgatei* has a low selfing rate, which limits expression of the high levels of inbreeding depression found in this species. As a consequence, the breeding system is stable despite the high inbreeding depression levels. *Schiedea lydgatei* is apparently moth-pollinated (Norman et al., 1997), and the occurrence of biotic pollination may be critical in the maintenance of high outcrossing rates and hermaphroditism.

The patterns of inbreeding depression, selfing rates, and allocation shifts in these six hermaphroditic and dimorphic species suggest that the evolution of dimorphism is associated with a shift to dry, windy habitats and the evolution of wind pollination in *Schiedea*. The colonization of windy, dry habitats appears to occur before changes in sex allocation. For most hermaphroditic species, the shift to dry, windy habitats apparently is associated with a loss of insect pollinators, resulting in an increase in the selfing rate. The increased selfing rate may result in greater expression of the high inbreeding depression rates found in these historically outcrossing populations. Under these conditions, females could be favored because they are obligately outcrossing, but only if pollination is not limiting populations (Weller et al., 1998). In these environments, the evolution of wind pollination may be followed by the rapid appearance of females in populations. Once females are introduced into the population, there is strong selection for different allocation patterns favoring hermaphrodites with greater male function. In these dry habitats, selection may act on traits associated with wind pollination and/or simultaneously on traits associated with resource allocation to increasingly male or female function.

GENETIC POTENTIAL FOR THE EVOLUTION OF DIMORPHISM

Theoretical models suggest that the evolution of dioecy may be favored because inbreeding depression levels and selfing rates are both high or because shifts in allocation of resources to a single sexual function result in accelerating fitness returns for individuals (Charlesworth & Charlesworth, 1978; Charnov, 1982; Lloyd, 1984). These accelerating fitness gain curves may result from a variety of ecological factors, including specific dispersal agents and shifts in pollinators (reviewed in Bawa, 1980; Lloyd, 1984; Thomson & Brunet, 1990; Sakai & Weller, 1999). In

Schiedea, shifts to wind pollination, as well as high inbreeding depression and high selfing rates, appear to be strong selective pressures favoring the evolution of gynodioecy and dioecy. The ability to respond to these selection pressures with further evolution of breeding systems will depend upon the genetic potential for changes in allocation to male and female function.

All of these models assume the existence of heritable genetic variation in patterns of allocation to male and female function. Genetic tradeoffs in allocation between the two sexual functions are also assumed (Stanton & Galloway, 1990; Charlesworth & Morgan, 1991; reviewed in Geber et al., 1999). Negative genetic correlations between male and female traits, such as stamen biomass and ovary biomass in hermaphrodites, may enhance the evolution of dioecy, while positive genetic correlations between these traits would impede evolution of dioecy and instead imply selection for larger or smaller flower size.

We know little about patterns of genetic variation and covariation in characters related to sex allocation for natural populations. Only a few recent studies have explored the quantitative genetics of sex allocation traits in hermaphroditic plant species (van Noordwijk & de Jong, 1986; Stanton & Galloway, 1990; Houle, 1991; O'Neil & Schmitt, 1993; Ågren & Schemske, 1995; Delesalle & Mazer, 1995; Mazer & Delesalle, 1996; Campbell, 1997; Mazer et al., 1999). These studies used controlled crosses to create families to estimate genetic variation and covariation of morphological characters, but they generally were not placed in a phylogenetic context. Other studies have examined the quantitative genetics of sex allocation traits in gynodioecious (Ashman, 1999, 2003; Delph et al., 2004, 2005), andromonoecious (Elle, 1998), and dioecious species (Meagher, 1992, 1994). Even fewer studies have examined the quantitative genetics of physiological traits in gynodioecious species (Poot et al., 1996; Caruso et al., 2003).

Closely related species of *Schiedea* with different proportions of females and with variation in male function in hermaphrodites should be especially informative in studies of the genetic changes underlying these sex allocation differences. In *Schiedea*, male sterility is controlled by a single nuclear gene (Weller & Sakai, 1991), but quantitative variation in other traits related to sex allocation in females and hermaphrodites is likely to be controlled by a number of genes. Some gynodioecious species may have breeding systems that are in transition, with allocation patterns that are under directional selection. Given this range of breeding systems and allocation patterns in such closely related species, we expect significant

heritability of biomass allocated to male and female function in gynodioecious species. Significant heritability of biomass would indicate the potential for evolutionary change, assuming that genetic correlations do not otherwise constrain the response. We have used a quantitative genetics approach to examine the genetic potential to evolve new breeding systems and traits related to allocation to male and female function in gynodioecious *S. salicaria*, a species with 13% females, and in *S. adamantis*, a species with 39% females.

We used heterozygous hermaphrodites and females as parents to generate families that would produce both hermaphrodites and female progeny. In *Schiedea salicaria*, thirty-five families (each consisting of one heterozygous hermaphrodite and one related female) were used in pollinations to produce the plants for a single generation experiment to estimate the heritabilities and genetic covariances for the focal traits. We employed a partial diallel design similar to that of Meagher (1992), but with larger sample sizes for greater statistical power. Each hermaphrodite was used as a pollen donor and crossed with three females randomly chosen from different families, and each female was crossed with three different unrelated hermaphrodites. In most cases, five females and five hermaphrodites from each sibship were measured for more than 30 traits. Additive genetic variances were estimated separately for females and hermaphrodites by examining the component of variation among paternal half-sib families using restricted maximum likelihood methods (see Kearsley, 1965; Shaw, 1987; Meagher, 1992). Narrow sense heritabilities were calculated for each trait in each sex as the additive genetic variance (four times the paternal variance component for this design) divided by the total variance (paternal variance + maternal variance + error; Falconer & Mackay, 1996). Genetic covariances and correlations were estimated separately for females and hermaphrodites, using best linear unbiased predictors (BLUPs) of sire breeding values obtained from our Proc Mixed analysis (SAS, 2001; Conner et al., 2003). Pearson correlation coefficients between BLUPs were calculated for each sex. The female and hermaphroditic data sets were also combined and Pearson correlation coefficients were calculated between homologous traits of the two sexes.

Heritabilities, and genetic correlations of females and hermaphrodites of Schiedea salicaria. Most floral traits show significant heritabilities in females and hermaphrodites. In general, the floral biomass of stamens (measured only in hermaphrodites) and carpels in both sexes shows high heritability. Fruit biomass is not heritable in terminal flowers, but is heritable in the more numerous lateral flowers in both

sexes (Sakai et al., unpublished). At the inflorescence level, both females and hermaphrodites exhibit high heritability in the number of flowers and fruits per inflorescence (Weller et al., in press). These results suggest that significant genetic variation is present in this species and that a response to selection could result in further differentiation of females and hermaphrodites, depending upon genetic correlations of traits.

Genetic correlations within hermaphrodites are unlikely to promote or hinder the evolution of dioecy in this species. Within hermaphrodites, female biomass (ovary, fruit, or seed) and male (stamen) biomass are independent of each other. Female biomass in females and male biomass in hermaphrodites also showed no genetic correlation, suggesting that specialization toward greater female function in females and greater male function in hermaphrodites would not be constrained. Other genetic correlations may impede selection for sexual dimorphism, with positive genetic correlations between similar traits in females and hermaphrodites. For example, the female biomass of females and of hermaphrodites is significantly genetically correlated, making specialization more difficult (Sakai et al., unpublished).

Schiedea salicaria has likely undergone a recent transition from biotic to abiotic wind pollination, and significant narrow-sense heritabilities were detected for inflorescence condensation and other traits related to wind pollination in *Schiedea* species (Weller et al., in press). Heritabilities were generally higher in hermaphrodites than in females. The presence of significant narrow-sense heritabilities for traits associated with wind pollination suggests that selection for more effective wind pollination in the windy, pollinator-limited environments where *S. salicaria* grows could lead to the evolution of the highly condensed inflorescences characteristic of other wind-pollinated species of *Schiedea*. A recent study of eco-physiological traits of *S. salicaria* and *S. adamantis* showed few differences between females and hermaphrodites, but significant narrow sense heritabilities for stomatal conductance and specific leaf area, suggesting that these traits could also respond to selection (Culley et al., 2006). Further analyses of traits related to floral and inflorescence architecture, wind pollination, and physiology should clarify how other genetic correlations may affect the evolution of dioecy in this species.

CONCLUSIONS

A multi-disciplinary approach, including phylogenetic analysis, population biology, and quantitative genetics, has been instrumental in understanding both

the genetic potential for different breeding systems to evolve in *Schiedea* and the selective factors that have promoted speciation and shifts in breeding systems. Autogamy and dimorphism evolved independently several times in *Schiedea*, and diversification has been associated with changes in breeding system, pollination system, and habitat. In general, dimorphic species have evolved in dry, windy habitats and are wind pollinated, while autogamous species occur in wetter habitats. Dimorphic breeding systems may have evolved as a mechanism to promote outcrossing because of the expression of high levels of inbreeding depression resulting from high selfing rates that occur with the loss of pollinators related to a shift to drier habitats. Quantitative genetics studies suggest that most morphological traits associated with wind pollination and resource allocation are heritable and could respond to selection. Strong selection for outcrossing in dry habitats and for selfing in wet habitats suggests that a further response to selection in breeding systems and other traits is possible.

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